LOWER LLANDOVERY (SILURIAN) TRILOBITES FROM KEISLEY, WESTMORLAND

By J. T. TEMPLE

CONTENTS

SYNOPSIS

A trilobite fauna of Lower Llandovery (Silurian) age is described from Keisley, Westmorland (northern England). The fauna contains probably eight species, the uncertainty being due to the difficulty of drawing interspecific boundaries among Proetidae. Young stages of *Diacanthaspis sladensis* (Reed) and *Lichas laciniatus* (Wahlenberg) are described, the latter suggesting a revised interpretation of the origin of the lateral glabellar lobes in that species. The fauna has little in common with that of the underlying Keisley Limestone.

I. INTRODUCTION

In this paper are described the trilobites from the Lower Llandovery limestone at Keisley, Westmorland (grid reference NY 7136 2377), of which the brachiopods were described recently (Temple 1968). The stratigraphical position of the limestone appears to be conformably between the underlying Keisley Limestone and overlying shales of the *Monograptus atavus* zone, i.e., probably lowest Silurian.

The trilobites, which are all disarticulated and preserved as moulds in the weathered limestone, are far less abundant than the brachiopods and, although well preserved, have suffered distortion more commonly than the brachiopods which are rarely distorted. Many specimens are incomplete, apparently as a result of breakage : this is true particularly of the large *Lichas laciniatus* (large, that is, by the standards of the other trilobites in the fauna, but small in comparison with Swedish material of the species), and of the proetids, in which the occipital ring is rarely preserved intact.

The terminology used is largely that of the *Treatise on Invertebrate Paleontology, Part O*, although the term *glabella* is used to include the occipital ring. The notation for the glabellar lobes (L) and furrows (S) numbered from back to front is that of Jaanusson (1956). The *lateral glabellar lobes* of *Lichas* are so called as their ontogeny (see p. 213) does not suggest that they are of composite origin. Shaw & Ormiston's (1964) term *eye socle* is used for the rim of free cheek immediately beneath the visual surface.

Registration numbers of specimens prefixed by A are those of the Sedgwick Museum, Cambridge, those prefixed by It of the British Museum (Natural History), London, that prefixed by ar. of the Palaeontological Institute, Uppsala, that prefixed by G of the National Museum of Ireland, Dublin.

II. TAXONOMIC PROCEDURE

The taxonomic treatment is similar to that adopted for the brachiopods (Temple 1968 : 3). It is considered that measurements should form the basis of the description and comparison of samples of fossil species ; and that only those species based on quantitatively described topotype samples of adequate size can be considered to be well established. The arbitrary criterion of sample sufficiency adopted is not less than ten specimens of (in trilobites) whichever part of the integument includes the holotype and on each of which all of four or more variates can be measured.

The greater complexity of trilobite than brachiopod skeletons leads to an embarrassingly greater choice of measurable variates. The procedure adopted here may in some cases err on the side of too extensive measurement: this seems, however, to be inevitable until experience has shown how many (and which) variates are needed to distinguish between, for instance, allied species of *Diacanthaspis* or *Flexicalymene*.

The ultimately subjective basis of the recognition of specific limits in a fossil sample (Temple 1968) constitutes a practical difficulty in the present fauna only in the case of the Proetidae, and to a lesser extent *Otarion*. The Keisley proetids (like the enteletaceans among the brachiopods) appear to show considerable shape variation, and there seems to be no way of deciding if this is inter- or intra-specific, especially as the numbers of specimens are too few for discontinuity of shape variation to be demonstrated. The other trilobites fall into six species, of which four are compared with earlier established species—*Diacanthaspis sladensis* (Reed), *Lichas laciniatus* (Wahlenberg), *Otarion megalops* (M'Coy) and *Dalmanitina mucronata brevispina* Temple. The original material of these species has been examined and measurements are given here, but in all cases the topotype samples are small and do not fulfil the criterion of sample sufficiency, so that the names of these species can be used at present only informally. The Keisley samples are also small, only that of *Diacanthaspis sladensis* consisting of more than ten adequately preserved specimens. Quantitative comparisons of the Keisley material are therefore hampered on both sides by small numbers.

Semi-quantitative comparisons of Keisley material with topotype specimens of *Diacanthaspis sladensis* and *Otarion megalops* have been made by plotting individual specimens on the shape eigenvectors (Temple 1968 : 6) of the variance-covariance matrices of the Keisley specimens (Text-figs. 1 and 4). In this way multivariate shape variation can be reduced to two dimensions, and the mutual relations of two samples and the continuity or discontinuity of their shape variation can be assessed visually. The direction of maximum shape difference between two samples can be calculated (Burnaby 1966 : 99) as the projection of the line joining their means on to the "plane" orthogonal to the size eigenvector of the Keisley sample (see pp. 210, 223).

III. MEASUREMENTS

Shaw, in a forward-looking article (1957), has discussed the problem of measuring trilobites and has suggested a standardised set of symbols for measurements. The attempted application of Shaw's symbols, however, raises immediately the problem of projection. Shaw projected on to the plane defined by the palpebral lobes, but in many cases (e.g. *Flexicalymene* and *Diacanthaspis* here) the palpebral lobes are too small, even if adequately preserved, to define a plane accurately—and of course in several trilobite families they are absent. An alternative is to project on to a "horizontal" plane at right angles to that passing through the posterior margin of the occipital ring (Whittington & Evitt 1954 : 11). In this case also there is considerable uncertainty about the exact orientation of the plane so defined, because the posterior margin of the occipital ring rarely lies exactly on a plane. The course adopted in most instances in the present work is to project on to the symmetrical plane defined by the "normal" projection of the sagittal cranidial length, i.e. at right angles to the straight line joining the midpoint of the anterior margin of the cranidium to the midpoint of the posterior margin of the occipital ring. Any departure from projection on to this plane is explicitly noted in the measurements given, as for instance in *Diacanthaspis* where measurements of the distances between paired glabellar spines are given as normal projections of themselves so as to be mutually comparable. For pygidia, projection is on to the plane defined by the lateral and posterior pygidial margins (as Shaw), or, if this plane is not definable, on to the plane defined by normal projection of the sagittal pygidial length. Shaw's symbols have not been quoted, in spite of the advantages of standardisation, so as to avoid confusion with his differently projected measurements.

Where possible, measurements have been made on external moulds, both in order to provide measurements that can be compared with those made on testiferous material, and because the furrows that define many measurements are usually sharper and thinner externally than internally. When, because of scarcity of external moulds, measurements have to be made on internal moulds, overall lengths and widths include the thickness of the integument, unless explicitly stated otherwise. Furrows are measured at the deepest points of their cross-sections. Measurements are quoted in mm. Doubled half-values of nominally symmetrical structures are printed in parentheses. Measurements of holotypes or lectotypes are printed in bold type. Specimens which have suffered distortion are indicated by an asterisk at the beginning of the line of measurements. In obliquely distorted specimens sagittal and exsagittal measurements have been made parallel to the distorted axial line and not at right angles to transverse measurements.

IV. FREQUENCIES OF SPECIES

The numbers in Table 1 are based on the specimens collected during the first and second counts of the brachiopods (1968 : 9, Table 1). They are less accurate than the brachiopod figures as they record only retained material and exclude the poorly preserved specimens transitorily exposed during preparation. Except for this slight downward bias the figures are comparable with the " combined count " brachiopod figures, so that for instance the frequencies of combined cranidia and pygidia can be compared with the frequencies of combined pedicle and brachial valves of brachiopods (*op. cit.*, Table 1, column 7). *Diacanthaspis sladensis*, the most common trilobite, is seen to be about as abundant in the whole Keisley fauna as *Salopina* sp. nov., the fourteenth most common brachiopod species.

TABLE I.
Frequencies of species

	Cranidia	Free cheeks	Hypostomes	Pygidia	Protaspides
Diacanthaspis sladensis	18	2	3	3	0
Lichas laciniatus	8	2	2	1	0
Proetidae	8	5	1	9	0
Otarion megalops	4	0	0	1	0
Flexicalymene sp.	4	2	2	4	0
Dalmanitina mucronata brevispina	1	1	0	2	1

Note. No specimens of *Aulacopleura* sp. were found during the counts on which the figures in the table are based.

V. DISCUSSION OF FAUNA

The Keisley Lower Llandovery trilobite fauna is small, consisting probably of eight species, although, as trilobites are rare in the Keisley Lower Llandovery as a whole, the proportion of species undiscovered by collecting may be relatively high. Certainly the list of families which occur in both Ordovician and Silurian strata but which have not been found in the present fauna is impressive—illaenids, harpids, raphiophorids, cheirurids, thysanopeltids, encrinurids, homalonotids, and phacopids ; and of these missing families the first four are known from the underlying Keisley Limestone (Reed 1896 : 408). On the other hand the Keisley Lower Llandovery trilobite fauna is somewhat richer than that of the presumably slightly earlier *Hirnantia* fauna which, at its richest in Bohemia, has only three species (Havlíček & Vanek 1966 : 61).

The known affinities of the trilobites are mostly with forms of closely similar or slightly earlier age: *Diacanthaspis sladensis* occurs in the St. Martin's Cemetery Beds of South Wales, the published fauna of which (Reed 1907 : 537) suggests that it is coeval with the Keisley fauna; *Lichas laciniatus* is from the Dalmanitina Beds of Västergötland, also probably close in age; *Dalmanitina mucronata brevispina* occurs in basal Silurian strata in Yorkshire (Temple 1952; 14); *Otarion trigoda* is from the presumably slightly earlier (Upper Ordovician) Boda Limestone of Dalarne. Only *Otarion megalops* suggests comparison with younger strata, M'Coy's species coming from rocks of probably Upper Llandovery age in Galway (Whittington & Campbell 1967 : 461).

It is interesting that there is little affinity between the Keisley Lower Llandovery trilobites and those of the underlying Keisley Limestone, only *Lichas laciniatus* being common to the two faunas (Warburg 1925 : 300). Reed's record (1896 : 411) of '*Calymene blumenbachi* var. *caractaci*' from the Keisley Limestone might suggest comparison with *Flexicalymene* sp. here, but the cranidium in question (A 11781) appears to be referable to *Diacalymene*, while the pygidium (A 11782 a, b) is very poorly preserved.

VI. ACKNOWLEDGMENTS

I am indebted to several persons for assistance, which is gratefully acknowledged: Sir James Stubblefield, F.R.S., and Mr. R. P. Tripp have read and commented on the manuscript; Mr. A. G. Brighton, Dr. W. T. Dean, Mr. C. E. O'Riordan and Dr. Anders Martinsson have made specimens available for study; the calculations have been facilitated by programs written by Mr. M. R. Farmer and Mr. E. G. Dee; the photographs are the work of Mr. M. S. Hobbs; technical assistance has been given by Mr. K. R. Coventry; the material was collected with the help of a grant from the Central Research Fund of London University.

VII. SYSTEMATIC DESCRIPTIONS

Family **ODONTOPLEURIDAE** Burmeister 1843
Genus ***DIACANTHASPIS*** Whittington 1941

Type species. *Diacanthaspis cooperi* Whittington 1941 by original designation of Whittington (1941 : 501).

Diacanthaspis sladensis (Reed 1905)
(Pl. 1, figs. 1–22)

1905 *Acidaspis sladensis* Reed : 100, pl. 4, figs. 8–12

Lectotype (here selected). Internal and external moulds of cranidium, A 4646 a, b figured by Reed, 1905a, pl. 4, fig. 8 (Pl. 1, figs. 17–18 here), from St. Martin's Cemetery Beds, Haverfordwest, Pembrokeshire, Wales.

Description (of Keisley material). *Cranidium*: Longitudinal convexity strong. Axial furrows distinct opposite glabellar lobes, indistinct opposite glabellar furrows. Glabella narrowing rapidly forwards from posterior margin to end of occipital furrow, then widening slightly around L_1 and S_1, narrowing again to the end of S_2

and then approximately parallel-sided. L_1 and L_2 stand only slightly above level of cheeks but central lobe of glabella has strong independent transverse and longitudinal convexity and becomes nearly vertical in front; central lobe narrows opposite L_1 and L_2, its outlining longitudinal furrows deepest opposite L_1; S_1 and S_2 oblique, S_1 deepened to a pit at its inner end, S_2 deepened along its length, both apparently apodemous; S_3 and small oblique L_3 rarely distinguishable. Occipital furrow broad and transverse behind central lobe, deepened and apodemous behind L_1 where it turns obliquely forwards; occipital ring wide (sag. & exsag.) behind central lobe, declining and narrowing rapidly distally as posterior margin strikes obliquely forwards to axial furrow; faintly cut-off occipital lobes; in large specimens a furrow curves around from inner ends of occipital lobes sub-parallel to margin of occipital ring, separating a narrow posterior strip which bears paired marginal spines and a small axial spine.

Fixed cheek highest opposite L_1, sloping very steeply backwards to posterior border furrow and less steeply forwards; palpebral lobe elevated, opposite highest point of cheek. Eye-ridge extends in slight outwardly convex curve to anterior end of axial furrow; eye-ridge bounded internally by parallel furrow ending in slight depression at axial furrow; cheek within furrow semicrescentic in front of palpebral lobe and with independent convexity. Anterior branch of facial suture diverges from eye-ridge progressively forwards across deep wide concave intervening strip on to anterior border; posterior branch of facial suture runs in sinuous curve to just within genal angle; both branches apparently run along sutural ridges. Anterior border sub-horizontally disposed relative to plane tangent to posterior part of glabella, narrowest axially. Posterior margin of cheek beyond axial furrow slopes obliquely back in slightly outwardly convex curve; posterior border furrow broad; posterior border roll-like and widening outwards.

Surface of cranidium (except for the various furrows including that beyond the eye-ridge) with spines of different sizes, regularly arranged in places, the most conspicuous being distributed as follows: occipital ring with strong posterodorsally directed paired marginal spines and small axial spine on posterior strip, strong axial and smaller paired flanking spines dorsally directed on anterior part; single row on eye-ridge; semi-crescentic cheek within eye-ridge bearing three rows posteriorly in large forms; strong paired glabellar spines which are conspicuous early in development (see below) are usually in large forms not easily distinguishable from subsequently developed glabellar spines which cover central lobe in more or less symmetrical pattern.

Free cheek: Eye elevated on vertical stalk; lenses visible on internal but not external moulds. Cheek slopes strongly down from base of stalk to broad border furrow beyond which border has strong independent convexity; border widening posteriorly. Librigenal spine deflected outwards from margin of cheek and curved convexly outwards, about as long as extreme oblique length of cheek. Margin of cheek with radially directed or sub-parallel spines wider and longer posteriorly; 11, 12, 13, 14 spines counted in 4 doubtfully complete cheeks; last spine (? more than one) on librigenal spine. On border a row of dorsally directed spines fewer than (8 counted on each of the same 4 cheeks) and not corresponding to marginal spines, and on large forms an internal row of smaller spines. Within border furrow scattered spines with smaller spines intercalated in large forms.

Hypostome: Outline sub-rectangular, ratio of minimum width to sagittal length averaging about 1·2 : 1; anterior margin convex; posterior margin shallowly indented axially; lateral margins indented. Middle body strongly outlined laterally and posteriorly, with paired furrows running obliquely back from just within anterior corners where they are wide and deep, dying out before mid-line; furrows define elongated posterior lobes confluent axially. Anterior border flat, narrowing out axially; posterior border wide, inclined gently upwards (ventrally); middle portions of lateral borders inclined more steeply upwards. Anterior lateral wings flat proximally, slightly declined (dorsally) distally; posterior lateral wings flattened relative to adjacent parts of borders. Surface bearing short spines. Doublure poorly known; dorsal surface apparently smooth.

Thoracic segments: The number of thoracic segments is unknown. Two types of isolated segment are known.

Type 1 (presumably anterior): Axial ring not known in detail but apparently with two (?) pairs of dorsally or dorsoposteriorly directed strong spines. Pleura horizontally disposed. Anterior pleural band narrow (exsag.), with 5 small hollow dorsally directed spines. Pleural furrow transverse; at its distal end is developed a hollow anterior pleural spine directed nearly straight downwards and curving slightly backwards. Posterior pleural band about as wide (exsag.) as combined anterior band and pleural furrow, raised, bearing two strong dorsally directed hollow spines, continued distally into horizontal transversely directed hollow posterior pleural spine from base of which arise a dorsolaterally directed spine and proximal to this a smaller spine more dorsally directed. Behind posterior band a narrow (exsag.) horizontal flange.

Type 2 (presumably posterior): Differs in the anterior pleural spine being directed nearly horizontally (only slightly backwards and downwards), and in the posterior pleural spine being directed postero-dorsoad-axially (so that in the single known specimen its broken tip lies behind and above the axial furrow) and without two spines at its base.

Pygidium: Outline roundedly sub-triangular, strongly elongated transversely, ratio of maximum width (at anterior margin) to sagittal length (both excluding spines) averaging about 3·6 : 1; ratio of width of axis to width of pygidium along anterior margin averaging about 0·3 : 1. Pleural lobes flat; axis defined by independent convexity but axial furrows not clearly marked except posteriorly. Articulating half-ring narrow; articulating furrow and ring furrow steepest anteriorly. Axis with two rings; first axial ring approximately parallel-sided, the central transverse strip independently raised; second ring narrower (tr.) but longer (sag. & exsag.), slightly indented axially behind, its posterolateral portions with slight independent convexity and forming in large specimens a bilobed terminal piece. Posterior margin with 7, 8, 9 spines on each side in 2, 6, 1 specimens; spines directed slightly dorsally initially but curving gently downwards, approximately radial to margin, equally spaced and of equal size except for most anterior one which is closer and smaller and squeezed in just within anterolateral corner of pygidium; third spine outwards from mid-line connected to first axial ring by faint pleural rib. Pleural rib sharply geniculated a short distance away from axial furrow; behind geniculation pleural rib runs sub-parallel to axial line or slightly postero-adaxially in outwardly slightly concave curve. Dorsal spines distributed as follows: on first ring and on anterior part of second ring a strong pair and up to 2 (in largest specimen) flanking pairs in transverse line; sagittal spines (in largest specimens) at fronts of first and second rings and immediately in front of furrow behind second ring (between lobes of " terminal piece "); on each pleural lobe one strong spine near geniculation of pleural rib, 2 others (3 in largest specimen) diminishing in size in approximately transverse line outwards, 3 small spines in front near anterior margin and (in largest specimen) 2 small spines behind; one each at bases of proximal marginal spines (up to sixth outwards in largest pygidium). Doublure directed obliquely down and inwards from margin.

Outer surface of cephalon and pygidium: Finely granular between spines.

MEASUREMENTS.

Cranidium (all lengths except no. 6 measured as normal projections)

1 = sagittal length of glabella (exclusive of axial occipital spine)
2 = sagittal length of occipital ring (exclusive of axial spine)
3 = sagittal length of preoccipital glabella
4 = mid-point of S_1 to midpoint of lateral part of occipital furrow (exsag.)
5 = mid-point of S_2 to midpoint of S_1 (exsag.)
6 = mid-point of occipital furrow to midpoint of palpebral lobe (exsag.) (projected normal to plane tangent to glabella on either side of occipital furrow)
7 = width of glabella (maximum) across L_1
8 = width of glabella at midlength of L_2
9 = width of frontal lobe of glabella
10 = minimum width of central lobe of glabella (opposite L_1)
11 = transverse separation of midpoints of outer edges of palpebral lobes
12 = base of paired occipital spine to base of spine 2a (exsag.)
13 = base of spine 2a to base of spine 2 (exsag.)
14 = base of spine 2 to base of spine 3 (exsag.)
15 = base of spine 3 to base of spine 4 (exsag.)
16 = base of spine 4 to base of spine 5 (exsag.)
17 = transverse separation of bases of paired occipital spines
18 = transverse separation of bases of spines 2a
19 = transverse separation of bases of spines 2
20 = transverse separation of bases of spines 3
21 = transverse separation of bases of spines 4
22 = transverse separation of bases of spines 5

N.B. The tops of the palpebral lobes are often missing, in which case 6 and 11 are estimates. Bevelling of the corners of the central lobe of the glabella makes 10 difficult to measure consistently.

Variates	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Individual	0·44	0·10	0·34	—	—	—	—	—	0·21	0·12	—	—	—	0·08	0·12	—	—	—	0·07	—	0·06	—
specimens	0·58	0·15	0·46	0·15	0·15	0·27	0·39	0·39	0·36	0·24	0·85	0·17	0·11	0·16	—	—	0·21	0·10	0·12	0·13	—	—
	0·80	0·16	0·64	0·19	0·17	—	0·48	0·46	0·39	0·28	—	—	0·15	0·17	0·19	—	—	—	0·16	—	0·16	—
	—	0·19	—	0·22	0·16	0·18	0·40	0·39	—	0·23	0·87	0·22	0·15	0·17	0·22	—	—	0·11	0·15	0·15	0·15	—
	* 0·92	0·22	0·73	0·22	0·21	—	—	0·59	0·51	0·30	—	0·29	0·13	0·18	0·22	0·10	0·29	0·23	0·17	0·19	0·19	—
	* —	0·32	0·70	0·22	0·19	—	0·53	0·48	—	0·29	—	0·30	0·16	0·19	0·22	—	0·32	0·18	0·18	0·19	0·18	—
	0·95	0·27	0·73	0·22	0·22	0·19	0·63	0·58	—	0·32	1·14	0·27	0·16	0·19	0·19	0·15	0·34	0·13	0·15	0·16	0·18	0·24
	0·95	0·22	0·75	0·19	0·21	—	0·48	0·46	0·48	0·27	—	0·27	0·15	0·18	0·21	0·10	0·24	0·12	0·17	0·17	0·21	0·22
	1·02	0·22	0·80	0·24	0·24	0·24	0·81	0·78	0·69	0·44	1·65	0·24	0·21	0·24	0·27	0·13	0·30	0·19	0·22	0·23	0·29	—
	1·04	0·22	0·82	0·34	0·17	0·19	0·61	0·53	0·52	0·32	1·21	—	0·18	0·18	0·27	0·15	0·36	0·12	0·16	0·16	0·17	0·24
	* 1·08	0·32	0·87	0·29	0·22	—	0·56	0·51	0·44	0·27	—	0·34	0·24	0·21	0·21	0·12	0·33	0·15	0·17	0·21	0·19	0·24
	1·16	0·29	0·90	0·27	0·24	0·36	0·89	0·79	—	0·51	(1·85)	0·34	0·18	0·19	0·34	0·15	0·44	0·22	—	0·19	0·22	0·32
	* 1·21	0·27	0·97	0·27	0·32	—	0·85	0·78	0·68	0·44	—	0·27	0·22	0·22	0·33	0·16	0·44	—	0·19	0·22	0·22	0·24
	1·21	0·29	0·97	0·29	0·29	0·25	0·90	0·85	0·68	0·51	1·94	0·30	0·23	0·27	0·28	0·12	0·48	—	0·27	0·28	0·30	0·25
	1·26	0·29	0·99	0·34	0·32	0·35	0·87	0·75	0·61	0·48	1·60	—	—	—	—	—	0·41	—	—	—	0·27	0·23
	1·31	0·32	1·02	0·30	0·30	0·27	—	—	0·63	0·48	1·75	0·36	0·22	0·29	0·29	0·16	0·41	0·28	0·21	0·19	0·22	0·30
	1·33	0·34	1·09	0·36	0·32	0·25	1·09	1·02	0·97	0·61	2·30	—	0·29	0·27	0·32	0·17	0·56	0·22	0·29	0·34	0·36	0·36
	1·33	0·36	1·01	0·39	0·33	0·25	0·99	0·95	0·78	0·52	1·85	0·41	0·22	0·32	0·24	—	0·56	0·17	0·32	0·40	0·36	—
	—	—	1·21	—	0·34	—	—	0·87	0·78	—	—	—	0·25	0·33	0·36	0·21	—	0·18	0·27	0·29	0·32	0·35
	—	—	1·21	0·42	0·39	0·40	1·19	1·09	0·97	0·61	—	0·39	0·30	0·30	0·36	0·19	—	0·39	0·32	0·24	0·34	0·41
	1·58	0·41	1·31	0·42	0·39	0·25	1·02	0·90	0·82	0·56	1·90	0·48	0·27	0·33	0·34	0·21	0·56	0·29	0·29	0·29	0·30	0·34
	—	—	1·31	0·53	0·36	0·25	1·21	1·07	0·92	0·63	—	0·53	0·30	0·27	0·39	0·21	—	0·15	0·30	0·30	0·36	0·40
	* —	0·44	—	0·41	0·39	—	1·14	1·02	0·90	0·55	—	0·51	0·29	0·32	0·34?	—	0·61	0·19	0·29	0·24	0·29	—
	* —	0·51	—	0·58	0·56	—	1·55	1·38	—	0·85	—	0·73	0·42	0·44	0·44	—	0·87	0·32	0·44	0·40	0·36	—
	1·96	0·36	1·58	0·48	0·44	—	(1·21)	(1·12)	—	(0·68)	—	0·48	0·33	0·33	0·45	0·27	—	0·27	0·29	0·32	0·34?	0·35
	2·40	0·58	1·84	0·61	0·45	0·45	1·55	1·33	1·15	0·91	3·10	0·61	0·41	0·44	0·51	0·27	—	0·42	0·48	0·46	0·46	0·47
	* —	0·58	1·99	0·68	0·61	0·60	2·23	1·89	1·58	1·31	4·35	0·61	0·48	0·55	0·61	0·34	—	—	—	—	0·58	0·65
	* 3·00	0·73	2·50	0·87	0·78	0·50	2·01	1·82	—	1·09	3·95	0·97	0·56	0·56	0·80	—	—	0·41	0·51	0·55	—	—
	3·55	0·75	2·90	1·00	0·95	—	2·75	2·40	1·90	1·30	—	—	0·50	0·75	—	—	—	0·55	—	0·80	—	—
sladensis	* —	—	2·15	1·05	0·65	—	2·20	2·00	—	0·80	(4·2)	0·70	0·45	0·70	—	—	0·80	0·40	0·60	0·65	—	—
topotypes	* **2·50**	**0·75**	**1·90**	—	**0·65**	**0·35**	**2·00**	**1·80**	**1·45**	**0·85**	**3·7**	**0·75**	**0·50**	**0·50**	—	—	**0·85**	**0·25**	**0·50**	**0·60**	—	—

Hypostome (all lengths projected as 23)
23 = sagittal length (normal projection)
24 = overall length (exsag.)
25 = sagittal length of middle body
26 = maximum width (at anterior wings)
27 = width at posterior wings
28 = minimum width

Variates	23	24	25	26	27	28
Individual	0·8	—	0·7	1·25	—	1·05?
specimens	1·05	1·1	0·85	—	1·4	1·25
	1·2	—	0·95	1·9?	1·75?	1·55
	1·25?	—	0·95	1·55	—	1·2
	1·25	—	1·05	—	1·9	1·75
	* 1·3	1·35	—	—	—	1·65
sladensis topotype	1·2	1·25	1·0	1·55?	1·45	1·3

Pygidium (all lengths projected on to plane of margin)
29 = sagittal length (exclusive of half-ring and posterior spines)
30 = overall length of axis (exclusive of half-ring) (sag. or exsag.)
31 = length (sag.) of first axial ring
32 = maximum width (exclusive of spines)
33 = width of axis at anterior margin
34 = transverse separation of bases of paired spines on first axial ring
35 = transverse separation of bases of paired spines on second axial ring
36 = transverse separation of bases of paired spines at geniculations of pleural ribs
37 = base of paired spine on first axial ring to base of paired spine on second axial ring (exsag.)
38 = transverse separation of bases of third (from axial line) marginal spines

Variates	29	30	31	32	33	34	35	36	37	38
Individual	0·6	0·55	0·25	—	0·65	0·25	0·15	0·8	0·25	0·8
specimens	0·6	0·55	0·25	—	0·7	0·25	0·15	0·9	0·25	0·85
	0·65?	0·5	0·2	2·7?	—	—	0·2	1·05	0·2	1·0
	0·65	0·6	0·25	2·6?	0·9	0·25	0·25	1·15	0·25	1·05
	0·7	0·55	0·25	2·3	0·8	0·25	0·25	1·0	0·25	0·95
	0·8	0·65	0·3	(*3·15*)	0·9	0·3	0·25	1·2	0·3	1·2
	0·8	0·7	0·3	2·25?	0·75	0·25	0·2	1·05	0·35	1·1
	—	0·7	0·35	—	1·0?	0·3	0·3	1·3	0·35	1·3
	1·05	0·9	0·4	3·85	1·25	0·45	0·3	1·65	0·4	1·7
sladensis topotype	0·85?	0·65	0·3	3·55	0·9	—	0·3	1·4	—	1·4

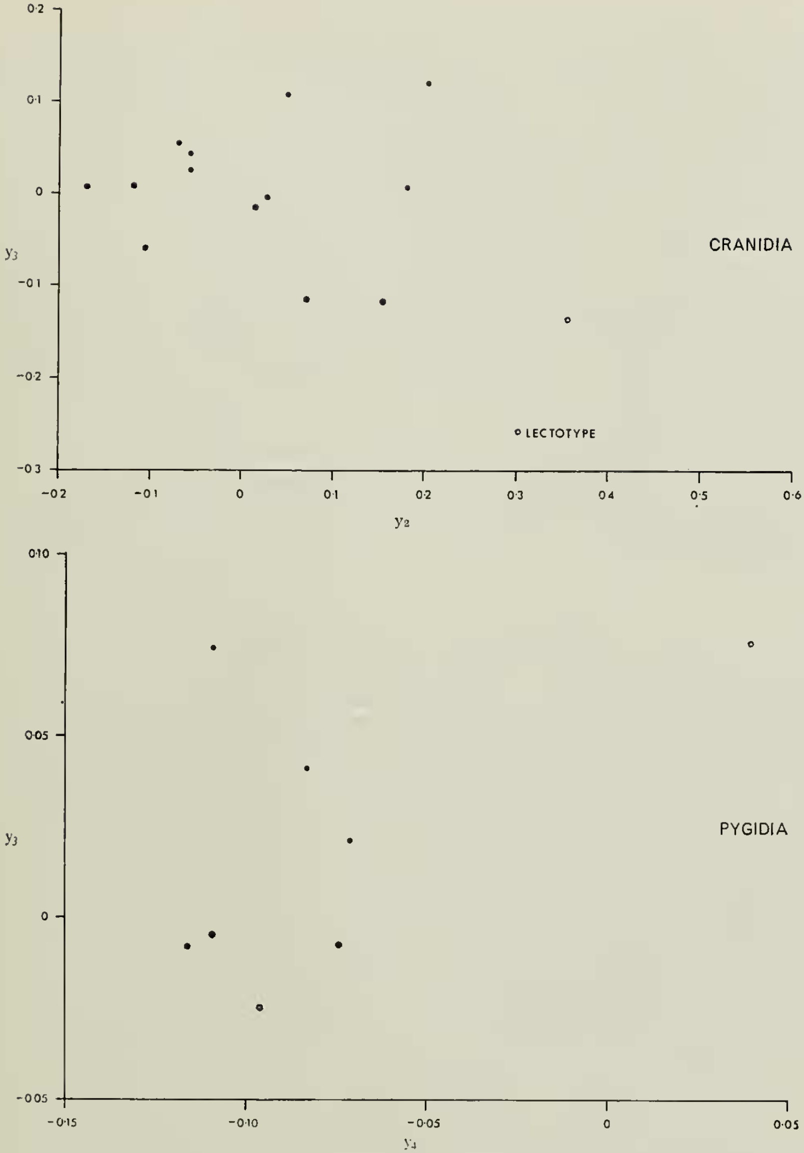

FIG. 1. Cranidia (above) and pygidia (below) of *Diacanthaspis sladensis* from Wales (open circles) and Keisley (closed circles) plotted on respectively the second and third (y_2 and y_3) and third and fourth (y_3 and y_4) eigenvectors of the variance-covariance matrices of the Keisley specimens. Transformed scale units correspond to original measurements in mm.

The scatters show the disposition of the Welsh and Keisley specimens relative to two of the axes of shape variation of the Keisley samples, the effects of size differences having been removed by, as it were, viewing the scatters down the first eigenvectors. See text for further details.

ONTOGENY. A cranidium of glabellar length 0·58 mm. shows spines on the occipital ring as described above except for lack of the pair of smaller flanking spines on the anterior part; on the central lobe of the glabella there are paired spines (notation after Whittington 1956: text-fig. 1) just in front of the occipital furrow (2a), opposite the inner ends of S_1 (2), and behind S_2 (3), pair 2 being closer to 2a than to 3, and further forwards an axial spine (beyond this the anterior part of the central lobe is poorly preserved), one spine on L_1, none on L_2, three strong spines proximally on fixed cheek (A_1, A_2, A_3) as well as more distal ones and a row of spines along posterior border. A cranidium of glabellar length 0·80 mm. (Pl. 1, fig. 12) is better preserved anteriorly and shows on the anterior part of the central lobe in front of the axial spine a pair of spines (4) and then a row of three spines (5); it has a full complement of occipital spines and there is an incipient axial spine opposite the posterior end of L_2 which has itself acquired a small spine. By a glabellar length of 0·95 mm. some spines have appeared laterally on the central lobe, and at a length of 1·02 mm. a row of three spines has appeared on the central lobe opposite L_1 which now has two spines.

In the smallest assigned hypostome (0·8 mm. long) the paired furrows are very deep anteriorly.

Of the two flanking pairs of tubercles on the pygidial axial rings the proximal pairs appear first, and of those pairs that on the second ring appears before that on the first.

REMARKS. The original type material of *D. sladensis* (refigured here on Pl. 1, figs. 17–21) consists of two cranidia and a pygidium, together with some associated material not described by Reed. Among the latter are a hypostome, a free cheek and two pleural fragments, all on the same block as the lectotype cranidium. The lectotype shows better-developed S_3 and L_3 than any of the Keisley specimens, but the pygidium (with 8 pairs of marginal spines) appears to be very similar to those from Keisley. The associated Welsh hypostome, free cheek (which has 13 visible marginal spines and another on the librigenal spine) and pleural fragments are also very similar to their Keisley equivalents. The Welsh material is too scanty for a detailed quantitative comparison, but informal comparisons of the cranidia and pygidia can be based on shape variation (Text-fig. 1). For cranidia the plot is of the scores of 13 Keisley specimens and two *sladensis* syntypes (one being the lectotype) on the second and third eigenvectors of the variance-covariance matrix of the Keisley specimens based on variates 3, 5, 7, 8, 10, 12, 13, 14, 18, 19, 20 (the choice of variates is dictated by missing observations in the measured sample). It will be seen that for both y_2 and y_3 the scores of the two Welsh syntypes lie beyond the range of variation of the Keisley sample. The direction cosines of the maximum shape difference between the samples are (−0·48, −0·02, 0·44, 0·44, −0·45, −0·19, −0·05, 0·19, −0·20, 0·10, 0·24): Welsh glabellas are relatively shorter, wider across L_1 and L_2, and with a narrower central lobe. The principal component analysis of pygidia, which is based on variates 29, 30, 31, 33, 35, 36 and 38, shows that the single available Welsh specimen is not separable from Keisley specimens on y_2 but has scores beyond the Keisley range for y_3 and y_4. The direction cosines of the maximum shape difference are (−0·11, −0·52, −0·16, −0·63, 0·22, 0·37, 0·33): the Welsh pygidium has a narrower and shorter axis but more widely separated pleural ribs and third marginal spines.

Despite these detailed differences the overall resemblances of the Keisley and Welsh specimens are sufficient to justify reference of the former to *sladensis*. Reed's species is referred for convenience to *Diacanthaspis* pending clarification of the relations within the Odontopleurinae, because of the relative complexity of the occipital ring, the spininess of the dorsal surface, and the absence of major pygidial spines. Kielan (1960 : 106) has remarked on the difficulty of distinguishing *Diacanthaspis* from *Primaspis*, and to this may be added the difficulty of distinguishing *Diacanthaspis* from *Xanionurus* Whittington & Campbell (1967 : 478) and also from *Odontopleura* itself, of which the holotype of the type species has recently been redescribed (Bruton 1967 : 216). The genera of Odontopleurinae have been narrowly interpreted since R. & E. Richter's (1917) revision, but objective generic distinctions (if any such exist in the subfamily) have not yet emerged.

Family **LICHIDAE** Hawle & Corda 1847

Genus ***LICHAS*** Dalman 1827

TYPE SPECIES. *Entomostracites laciniatus* Wahlenberg, 1818, by original designation of Dalman (1827 : 71).

Lichas laciniatus (Wahlenberg, 1818)

(Pl. 2, figs. 1–14; Pl. 3, figs. 1–10)

1818 *Entomostracites laciniatus* Wahlenberg : 34, pl. 2, fig. 2*.
1925 *Lichas laciniatus* (Wahlenberg); Warburg : 295, pl. 8, figs. 14–18, 20, ?19, text-fig. 20.
1939 *Lichas laciniatus* (Wahlenberg); Warburg : 15, pl. 9, figs. 1–8.

HOLOTYPE. Pygidium, ar. 1, figured by Wahlenberg, 1818, pl. 2, fig. 2* (Pl. 3, fig. 5 here), from the Dalmanitina Beds, Bestorp, Mösseberg, Västergötland, Sweden.

DESCRIPTION (of Keisley material). Detailed description is given only of the free cheek and hypostome. The pygidium is apparently identical with Warburg's description, and the slight differences in the cranidium are discussed below.

Free cheek: Visual surface reniform, its long axis inclined anteriorly inwards, convex laterally but almost vertical overall so that lowest parts are slightly overhung; lenses visible on both internal and external moulds. Eye socle beneath eye vertical, bounded outside by furrow. Free cheek beyond furrow sloping, outwardly convex. Lateral border furrow represented by change in slope within lateral border. Lateral border almost flat, nearly horizontal, widening posteriorly but becoming indistinguishable before reaching posterior border. Lateral margin well-defined and angular in section. Posterior border furrow broad, curving backwards and directed centrally down librigenal spine so that posterior border narrows at its distal end. Librigenal spine strong, tapering rapidly, its outer margin continuing line of cheek margin. Posterior border with slight independent convexity. Lateral doublure steeply inclined at margin, rapidly becoming nearly flat and slightly outward-sloping proximally, reaching about to lateral border furrow, widening posteriorly and with terraced lines curving inwards at posterior margin (6 & 9 terraced lines observed opposite end of posterior border furrow on two specimens). Anterior facial suture running in outwardly convex curve to become almost tangential to margin in approximately exsagittal line with anteroproximal extremity of eye. Posterior facial suture directed almost transversely away from eye and then in an oblique outwardly convex curve. Free cheek (except furrow beyond eye socle) with low tubercles of different sizes affecting both surfaces of test, smaller on eye socle and becoming smaller and sparse towards lateral margin.

Hypostome: Outline evenly rounded anteriorly, axially indented posteriorly. Transverse convexity greatest across anterior lobe of middle body. Middle furrow directed back at about 45° to axial line, branching shortly inwards; anterior branch dying out before axial line but connected by a depression across middle body; posterior branch nearly parallel to adjacent part of lateral furrow, dying out shortly; intervening lobe with slight independent convexity. Lateral furrow deepest at end of middle furrow, swinging out and shallowing around posterior lobe, commonly branching obscurely before dying out before axial line. Border narrowing out rapidly around front of middle body, widening posteriorly; border continuous posteriorly with middle body. Opposite anterior lobe of middle body the distal edge of border is downturned (dorsally) to form small anterior wing; near end of middle furrow the downturned part becomes completely overturned to form behind this region the doublure of posterolateral border. Posterior doublure nearly flat, with (at head of embayment) a strong axial boss sharply delimited in front by a deep furrow separating it from anteriorly extended inner axial part of doublure which slopes steeply up (ventrally) to near surface of hypostome. Ventral surface of hypostome and dorsal surface of doublure smooth except for terraced lines on border and anterior wing near anterior lobe of middle body.

Thoracic segment: The pleural furrow is steep-sided anteriorly; beyond the fulcrum it becomes shallower and is directed down the middle of the pleural spine.

Pygidium: The pygidial doublure lies close and parallel to the dorsal surface; it widens slightly backwards and has 9 terraced lines posteriorly on a pygidium about 5·0 mm. long.

MEASUREMENTS.

Cranidium

1 = sagittal length (normal projection)
2 = preoccipital sagittal glabellar length (normal projection)
3 = minimum width (tr.) of central lobe of glabella, measured if necessary midway between turning points of left and right lateral furrows
4 = width (tr.) of left lateral lobe measured along continuation of line of 3
5 = width (tr.) of right lateral lobe measured along continuation of line of 3
6 = maximum width of glabella (across lateral lobes)
7 = width of glabella across widest part of frontal lobe
8 = mid-point of occipital furrow to anterior end of lateral lobe (exsag.) (projected as 2)

Variates		1	2	3	4	5	6	7	8
Individual		1·1?	0·85	0·19	0·07	0·09	0·36	0·41	0·27
specimens	*	1·75	1·3	0·35	0·2	0·2	0·85	0·85	0·7
	*	3·15?	2·55	0·65	0·65	—	—	2·15	1·5
	*	—	—	0·7	—	0·6	—	—	—
		—	2·8	0·75	0·75	0·75	2·65	2·5	1·6
	*	—	2·4?	1·0	0·85	1·0	3·3	—	1·4
	*	—	—	1·1	—	1·05	—	—	—
		—	—	1·1	0·9	0·75	—	—	—
		—	—	1·4	1·2	—	—	—	—
		5·25	4·15	1·4	1·35	1·4	5·0	4·7	2·55
		—	5·8	1·25	1·15	—	4·15	3·85	3·8
		—	6·5	1·75	—	1·5	—	—	4·5

Hypostome (all lengths projected as 9)

9 = sagittal length (normal projection)
10 = overall length (exsag.)
11 = mid-point of anterior margin to inner end of anterior branch of middle furrow (exsag.)
12 = maximum width
13 = minimum width
14 = maximum width of anterior lobe of middle body
15 = maximum width of posterior lobe of middle body

Variates		9	10	11	12	13	14	15
Individual		2·1	2·25	1·2	—	—	1·3	1·35
specimens	*	2·8	—	1·7	3·1	2·25	1·85	2·0
	*	5·25	—	3·15	(5·6)	—	3·6	—

Pygidium (all measurements projected normally)

16 = sagittal length exclusive of articulating half-ring
17 = maximum width
18 = width of axis at anterior margin
19 = minimum transverse separation of post-axial furrows
20 = posterior margin to position of minimum transverse separation of post-axial furrows (sag.)

Variates	16	17	18	19	20
Individual	1·8	—	0·95	0·55	0·95
specimens	4·35	—	(2·25)	1·15	2·15
laciniatus holotype	**17·4**	**(26·8)**	**8·9?**	**4·9**	**10·4**

Ontogeny. A cranidium 1·75 mm. long (Pl. 2, fig. 12; Text-fig. 2*b*) differs from larger specimens in having a relatively narrower glabella with proportionately shorter (exsag.) lateral lobes which reach only as far forwards as the inner ends of the prominent eye-ridges; on the central glabellar lobe there is a transverse furrow (presumably S_1) at the posterior ends of the lateral lobes, and further forwards are traces of paired furrows (presumably S_2); the occipital lobes are faintly defined.

A cranidium about 1·1 mm. long (Pl. 2, fig. II; Text-fig. 2*a*) is referred to the species on the basis of the strong eye-ridge palpebral lobe and well developed frontal lobe of the glabella, features which preclude reference to any of the other trilobites in the fauna. In front of the occipital furrow are two transverse glabellar furrows (presumably S_1 and S_2) and traces of paired furrows (presumably S_3) near the ends of the eye-ridges. Oblique furrows run back from near the outer ends of S_2 to join S_1 and apparently continue faintly back to define small lobes. The occipital ring is poorly preserved. The glabella is widest across the frontal lobe, and the axial furrows are deepened and widened to form anterior pits at the anterolateral corners of the glabella.

FIG. 2. Outline drawings of small cranidia of *Lichas laciniatus*, ×25. *a*, It 5012 (see Pl. 2, fig. 11) ; *b*, It 5021 (see Pl. 2, fig. 12).

If the smaller of these two specimens is correctly referred to *L. laciniatus* it seems that the small lobes near the back of the pre-occipital glabella at this stage correspond to the lateral (' bicomposite ') lobes of later stages; and that during development the lobes grow rapidly forwards (presumably pushing the axial furrows outwards as they go), the anterior ends of the lobes reaching the ends of the eye-ridges at a cranidial length of 1·75 mm. and ultimately extending considerably further forwards (Pl. 2, fig. 9). The forward extension of the lateral lobes during growth is illustrated by Text-fig. 3, a plot of the exsagittal length of the lateral lobes (measurement 8) against the sagittal length of the pre-occipital glabella (measurement 2). The fitted regression line clearly does not pass through the origin (the intercept on the ordinate axis being significantly different from zero, $p < \cdot 005$ one-sided), and the ratio of lateral lobe length to pre-occipital glabellar length decreases with decreasing size, slowly at first and progressively more rapidly until the lateral lobe would disappear at a pre-occipital glabellar length of about 0·48 mm. No specimen as small as this has been found at Keisley but it is interesting to note that the only known lichad protaspis, which has a pre-occipital glabellar length of about 0·37 mm., has no lateral lobes (Whittington : 1957 : text-fig. 13). At the other end of the size range the cranidium of *L. laciniatus* figured in profile by Warburg (1939 : pl. 9, fig. 3a), which is over twice as long as the longest measurable cranidium from Keisley, has lateral lobes proportionately longer than those of the Keisley specimens; this specimen plots close to (slightly above) the continuation of the regression line of Text-fig. 3.

Although there is strong evidence from the 1·75 mm. stage onwards for the forward growth of the lateral lobes relative to the rest of the glabella, the evidence for the earlier development of the lobes rests on a single specimen, the 1·1 mm. cranidium. Further evidence about the rapid early changes in the lateral lobes is clearly desirable. Such evidence would be provided by cranidia intermediate in size between these two stages, and, since the ratio of their lengths is 1·53, it is likely that such an intermediate instar may exist.

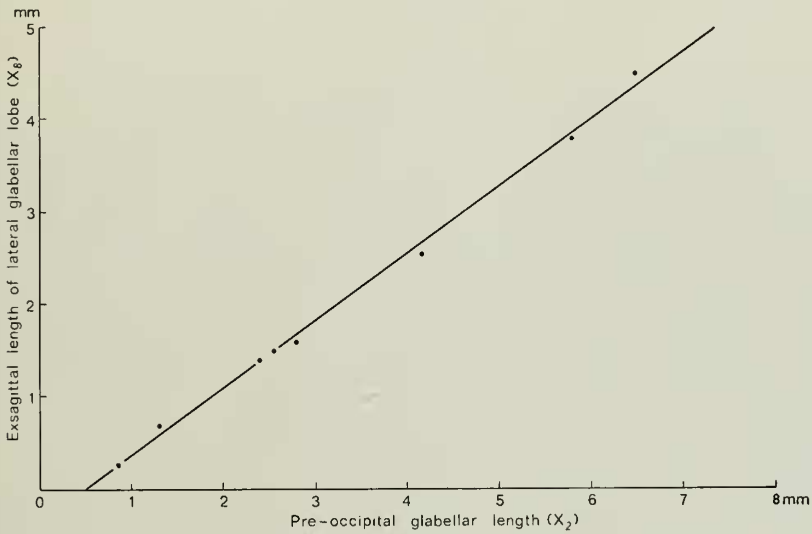

Fig. 3. A plot of measurements 8 and 2 on cranidia of *Lichas laciniatus* from Keisley. The fitted regression line has equation : $x_8 = 0{\cdot}726x_2 - 0{\cdot}350$.

The postulated development of the lateral lobes of *L. laciniatus* by forward growth from the back part of the pre-occipital glabella is quite different from the phylogenetic sequence normally assumed for the development of the lichad lateral lobes, i.e. by backward growth of the inner ends of S3 (Reed 1902 : 66).

Remarks. The strongly convex profile of the glabella, the relative width of the central lobe at its narrowest point (greater than the mean width of the lateral lobes measured along the same transverse line as the minimum central lobe width in 8 out of 10 specimens) and the relatively long axis of the pygidium suggest comparison of the Keisley material with *Lichas affinis* Angelin (see Warburg 1925 : 302, pl. 8, figs. 1–8, 11–13, 21, 23; 1939 : 16, pl. 9, figs. 13–15) rather than with *L. laciniatus*, as the two species have been interpreted by Warburg (1925 : 306). On the other hand, the neck of the central lobe is not raised above the lateral lobes and the post-axial furrows of the pygidium are not strongly divergent, features which are more suggestive of *L. laciniatus*, although the Keisley hypostome differs in its branched middle furrows from those attributed to either of the Swedish species. The Keisley material is referred to *L. laciniatus* because of the similarity of the pygidia to the holotype of Wahlenberg's species (Warburg 1939; pl. 9, fig. 1, refigured here as Pl. 3, fig. 5); quantitative comparison is precluded by the fragmentary nature of the Keisley material and the disparity in size with the much larger holotype.

Family **PROETIDAE** Salter 1864

Cranidium Type 1

(Pl. 4, figs. 1–4)

Description. Pre-glabellar area sub-horizontally disposed relative to tangent plane to posterior part of pre-occipital glabella; pre-glabellar field flat or slightly concave in section axially in front of glabella, becoming slightly convex abaxially; anterior border flat or slightly convex in section; anterior border furrow faint; pre-glabellar field usually slightly longer (sag.) than anterior border. Axial furrows not clearly incised around frontal lobe of glabella. Glabella widening slightly from occipital furrow around L_1, the effect being enhanced by bevelling and rounding of posterodistal corners of L_1. In front of L_1 glabella may appear slightly waisted but this is usually due to a point of inflection of the axial furrow rather than a true turning point. Glabella broadly rounded in front. S_1 very faint, inclined backwards but not circumscribing L_1; S_2 and S_3 not usually distinguishable with certainty but slight traces sometimes visible. Occipital ring narrowing (tr.) forwards and (exsag.) abaxially, bearing an axial tubercle and sometimes with traces of occipital lobes. Palpebral lobes poorly known, apparently long (extending from in front of S_2 to near posterior border furrows) and close to axial furrows. Pre-ocular facial sutures diverging usually strongly initially but converging near border furrow (sometimes almost at right angles to their earlier course) to cut margin along or within exsagittal line with front of palpebral lobe. Post-ocular fixed cheeks apparently very small and triangular. Outer surface of test smooth.

Cranidium Type 2

(Pl. 4, figs. 5–8, 12)

Description. Pre-glabellar area inclined obliquely downwards relative to tangent plane to posterior part of pre-occipital glabella; pre-glabellar field continuing slope of anterior part of frontal lobe of glabella, slightly convex in section; anterior border flat or slightly concave in section; anterior border furrow faint; pre-glabellar field usually slightly longer (sag.) than anterior border. Axial furrows clearly incised around frontal lobe of glabella. Glabella tapering forwards from just in front of occipital furrow, sometimes tapering less rapidly in front of S_2. Glabellar furrows well-marked: S_1 strong and oblique but not reaching occipital furrow; S_2 sub-parallel to S_1; S_3 short, less oblique, not reaching axial furrow. Occipital ring poorly known, bearing a small axial tubercle. Palpebral lobes poorly known, reaching apparently from about the ends of S_2 to near posterior border furrow. Preocular facial sutures and post-ocular fixed cheeks as in Type 1. Outer surface of test smooth.

Free cheeks

(Pl. 4, figs. 15, 16)

Two proetid and/or otarionid free cheeks are illustrated. It is not possible on the available material to demonstrate whether more than one type is represented.

Hypostome

(Pl. 4, figs. 9–11)

Description. Maximum width at anterior wings; outline waisted near mid-length. Anterior lobe of middle body very convex (but not pointed), sloping steeply from in front of its mid-length to anterior margin and more gently to middle furrow; anterolateral flanks of anterior lobe slightly bevelled. Middle furrow convex posteriorly, faint axially. Posterior lobe of middle body crescentic, continuing with slight independent convexity the downward (dorsal) backward slope of anterior lobe. Anterior border narrow (sag. & exsag.), upturned (ventrally). Details of anterior wings unknown. Lateral furrows absent opposite anterior wings; lateral and posterior furrows uniformly deep otherwise. Lateral border narrow, sloping up (ventrally) in side view to position opposite ends of middle furrows, sloping down behind around posterior lobe. Posterior border apparently sub-horizontally disposed, produced into 3 (?2) short spines on each side. Outer surface: anterior lobe of middle body with strong terraced lines diverging backwards from mid-line; lateral and posterior borders with strong terraced lines parallel to margin.

Pygidium Type 1

(Pl. 4, figs. 13, 20)

Description. Outline roundedly sub-triangular; ratio of maximum width to length about 1·4 : 1 in most complete specimen; maximum width situated slightly behind rounded anterolateral corners. Axis very convex, approximately semicircular in transverse section; axis forming 38% of maximum pygidial width at anterior margin of most complete specimen, tapering evenly backwards, not reaching posterior margin; posterior end of axis declining and ill defined, sometimes passing into slight tapering axial ridge. First axial ring well defined by sinuous ring furrow; six or seven further axial rings defined by thin sinuous ring furrows each of which is more steep anteriorly than posteriorly; terminal piece. Pleural lobes gently convex, without border. Sutural furrows very faint or indistinguishable; up to six pleural furrows distinguishable, wide, curved, extending almost to margin of pygidium, all except the first lagging progressively further behind corresponding axial rings; pleural furrows inclined obliquely backwards from axial furrows, the posterior ones progressively more so. Outer surface smooth, but one specimen shows faint traces of terraced lines on pleural lobes, and another shows terraced lines on axis.

Pygidium Type 2

(Pl. 4, fig. 17)

Three specimens differ from the above description in being more elongated transversely (ratio of maximum width to length 1·7 : 1 and 2·2 : 1 in two specimens), with a less convex axis, the oblique furrows being apparently fewer (only four observed on the only specimen with well-preserved pleural lobes) and directed initially more transversely away from axial furrows.

Pygidium Type 3

(Pl. 4, figs. 14, 18, 19)

Description. Outline imperfectly known, apparently sub-semicircular. Axis very convex, approximately semicircular in transverse section, apparently tapering only slowly for much of its length, not reaching posterior margin. Axis with 8 rings in best-preserved specimen. Pleural lobes gently convex; in some cases a barely perceptible distal change in slope forms an incipient border; up to 8 pleurae distinguishable; pleurae not lagging behind axial rings. Sutural furrows well marked, relatively thin and faint proximally but becoming stronger distally where they reach beyond ends of pleural furrows almost to pygidial margin behind raised distal ends of posterior pleural bands; pleural furrows narrower and more transversely directed than in Type 1; anterior pleural bands narrower (exsag.) than posterior bands along most of their length except towards margin where pleural furrows turn obliquely back before dying out.

A single specimen differs from the above description in being more transversely elongated and in having a wide tapering axis.

Measurements of proetidae.

Cranidium.

1 = sagittal length of glabella (normal projection)
2 = sagittal length of cranidium (projected as 1)
3 = sagittal length of occipital ring (projected as 1)
4 = sagittal length of anterior border (projected normal to sagittal length of pre-glabellar area)
5 = sagittal length of pre-glabellar field (projected as 4)
6 = maximum width of glabella
7 = maximum width (tr.) of occipital ring
8 = mid-point of occipital furrow to distal end of S_1 (exsag.) (projected as 1)
9 = mid-point of occipital furrow to distal end of S_2 (exsag.) (projected as 1)
10 = mid-point of occipital furrow to distal end of S_3 (exsag.) (projected as 1)

11 = transverse separation of distal ends of S_1
12 = transverse separation of distal ends of S_2
13 = transverse separation of distal ends of S_3

N.B. When the glabellar furrow does not reach the axial furrow the ' distal end ' in 8–10 and 11–13 is the point where the projection of the glabellar furrow along its distal length meets the axial furrow.

Variates		1	2	3	4	5	6	7	8	9	10	11	12	13
Individual specimens														
Type 1		1·1	1·5	0·25	0·15	0·3	0·75	0·65?	—	—	—	—	—	—
		1·2	1·65	0·25	0·1	0·3	1·0	—	0·35	0·55	0·65	0·95	0·8	0·7
	*	1·35	1·7	0·25	0·15	0·25	0·6	—	—	—	—	—	—	—
		1·85	2·35	—	0·55[a]	—	1·2	—	—	—	—	—	—	—
		2·25	2·9	0·45	0·65[a]	—	1·35	—	—	—	—	—	—	—
	*	2·3	3·0	0·5	0·3	0·35	1·75	1·6	0·6	1·0	—	1·65	1·5	—
	*	2·7	3·45	0·55	0·3	0·45	2·0?	—	0·75	1·25	1·6	1·9?	1·6	1·45
		3·4	4·25	0·6	0·5	0·45	—	—	—	—	—	—	—	—
Type 2?	*	1·95	2·6	0·35	0·3	0·45	1·1	—	0·6	0·85	1·05	1·0	0·85	0·85
		3·55	4·45	0·6	0·4	0·55	2·35	—	1·2	1·6	—	2·05	1·9	—
Type 2	*	0·8	1·1	0·1	0·2	0·2	0·6	—	0·25	0·35	0·45	0·6	0·55	0·55
	*	0·95	1·3	0·1	0·2	0·3	—	—	0·2	0·4	—	0·65	0·6	—
		—	—	—	0·2	0·35	—	—	—	—	—	1·05	0·95	0·85
	*	1·9?	2·5?	—	0·25	0·35	—	—	0·5	0·8	1·0	1·45	1·35	1·3
	*	2·05	2·8	—	0·35	0·5	—	—	0·5	0·95	—	1·5	1·35	—

[a] value for 4+5.

Hypostome (lengths projected normal to sagittal length).
1 = sagittal length
2 = anterior margin to posterior furrow (sag.)
3 = mid-point of anterior margin to position of minimum width (exsag.)
4 = width at anterior wings
5 = minimum width
6 = maximum width opposite posterior lobe of middle body
7 = minimum width of middle body
8 = maximum width of posterior lobe of middle body

Variates	1	2	3	4	5	6	7	8
Individual specimens	1·05	0·95	0·4	0·85?	0·6	0·7	0·45	0·6
	2·3	2·1	1·25	—	1·4	1·45	1·0	1·15
	2·8	2·55	1·55	—	—	—	—	—

Pygidium (lengths projected on to plane of margin).
1 = sagittal length excluding half-ring
2 = articulating furrow to ring furrow behind 5th axial ring (sag.)
3 = maximum width
4 = width of axis at anterior margin

5 = width of axis at ring furrow behind 5th axial ring
6 = score of 4th pleural furrow on scale of distal ends of ring furrows (articulating furrow counted as 1)
7 = width (perpendicular to length of pleura) of anterior band of 4th pleura at mid-length of pleura (projected normal to pleura)
8 = width (perpendicular to length of pleura) of posterior band of 4th pleura at mid-length of pleura (projected as 7)

Variates	1	2	3	4	5	6	7	8
Individual specimens								
Type 1	2·3	—	(3·55)	1·0	—	—	—	—
	5·4	2·85	7·7?	2·9	1·9	4·8	—	—
*	5·6	2·9	—	—	—	4·7?	—	—
Type 2	2·15	1·0	4·75?	1·45	0·9	5·0	—	—
*	2·7	1·5	4·7?	—	—	—	—	—
Type 3	1·25	0·7	2·4	0·6	0·35	4·2	—	—
	—	—	—	1·35?	0·95	4·3	0·19	0·23
	3·3	—	(4·6)	—	1·0	4·3	0·16	0·24
*	3·7	2·0	—	—	—	4·2	0·21	0·27

Remarks on proetidae. Analysis of the proetid material is difficult. Of the three morphological types of pygidia which can be distinguished, Types 1 and 2 differ mainly in their width-relations and variation in this character may prove with larger collections to be continuous between the two morphotypes, while Type 3 differs considerably from both the others in segmentation and in the nature of the pleurae. The three pygidial morphotypes may, therefore, reduce to two basic types. Among cranidia also, two main morphotypes may be recognized, but their distinction is difficult and doubtfully objective. Provisionally, though, it may be accepted that both cranidia and pygidia show two morphotypes. On the other hand it is not possible to distinguish two types of proetid hypostome among the four available specimens, while the numerous proetacean free cheeks cannot even be separated with certainty into proetid and otarionid.

Of the two proetid cranidial morphotypes, Type 1 may be referable to *Proetidella* (see Dean 1963 : 243), a genus which Whittington (1966 : 81) has recently considered a synonym of *Astroproetus*. Type 2 would seem on current taxonomic practice to belong to a different, apparently undescribed, genus, but the possibility cannot be excluded that it represents a different morph of the same species as Type 1. There is no evidence as to association of the two (or three) pygidial morphotypes with cranidia.

Family **OTARIONIDAE** R. & E. Richter 1926

Genus ***OTARION*** Zenker 1833

Type species. *Otarion diffractum* Zenker 1833, by subsequent designation of R. & E. Richter (1926 : 95).

Otarion megalops (M'Coy, 1846)

(Pl. 5, figs. 1–5, 7–13, 15–19, 21, 22, ?20)

1846 *Harpes* (?) *megalops* M'Coy : 54, pl. 4, fig. 5.
1967 *Otarion megalops* (M'Coy, 1846) ; Whittington & Campbell : 461, pl. 19, figs. 1–14, 16.

HOLOTYPE. Internal mould of cranidium, G 110 : 1967/3, figured by M'Coy, 1846, pl. 4, fig. 5, from Upper Llandovery of Boocaun, near Cong, County Galway, Eire.

DESCRIPTION (of Keisley material). *Cranidium*: Sagittal and transverse convexity strong; glabella with strong independent convexity. Pre-glabellar field long, convex in profile, sloping down forwards as a continuation of slope of anterior part of glabella. Anterior border furrow broad; anterior border convex in profile and nearly horizontally disposed. Relative dimensions of glabella are summarized in quoted measurements. Glabella broadly rounded in front (see also ' Remarks ' below). Basal glabellar lobes relatively small, delimited axially by furrows deeper than adjacent parts of axial furrows. A slight inward thickening of axial furrows shortly in front of basal lobes may represent S_2. Palpebral lobes long, reaching back almost to mid-length of basal glabellar lobes. Anterior branches of facial suture diverging variably anteriorly in outwardly convex curves. From front end of palpebral lobe a vague ridge (? eye-ridge) flanked externally by a shallow groove runs obliquely forwards to axial furrow at front of glabella. Dorsal surface smooth; axial tubercle on occipital ring.

Free cheek: Not identified.

Hypostome: A single large hypostome is tentatively associated with the cranidium of *O. megalops*. It is too incomplete to warrant detailed description but is similar to one of the otarionid hypostomes from the Silurian of Maine described by Whittington & Campbell (1967 : 464, pl. 7, figs. 21–22).

Pygidium: Outline transversely elongated (ratio of maximum width to length about 2·2 : 1 in two specimens), evenly rounded posteriorly. Axis forming about 25% and 30% of maximum width at anterior margin in two specimens, tapering sharply to narrow rounded termination, not reaching posterior margin, not strongly convex. Axis with 6 or 7 axial rings and small terminal piece; anterior ring furrows branch over axial line. Pleural lobes nearly flat; in two specimens out of three a faintly raised border; 5 (?6) pleurae visible, the first directed initially transversely away from axial furrows, subsequent pleurae directed increasingly backwards from axial furrows; pleurae not lagging behind axial rings. Sutural furrows relatively narrow proximally, becoming stronger distally where they reach beyond ends of pleural furrows almost to pygidial margin behind raised distal ends of posterior pleural bands. Pleural furrows broader (exsag.) than sutural furrows. Anterior pleural bands as wide (exsag.) as posterior bands adjacent to axial furrows, widening outwards to become wider than parallel-sided posterior bands. Outer surface smooth but axial rings bear sagittal tubercles.

MEASUREMENTS.

Cranidium

1 to 7 as for Proetidae (p. 218)
8 = minimum width of central lobe of glabella
9 = transverse separation of axial furrows at distal ends of S_1
10 = mid-point of occipital furrow to distal end of S_1 (exsag.) (projected as 1)

Variates		1	2	3	4	5	6	7	8	9	10
Individual	*	0·65	0·9	0·15	0·15	0·15	—	—	—	0·4	0·1
specimens		0·7	—	0·15	—	—	0·5	—	0·2	0·5	0·15
		1·05	1·5	0·15	0·15	0·3	0·7	—	0·35	0·6	0·35
		1·2	1·75	0·25	0·25	0·25	1·0	—	0·45	0·75	0·35
		1·25	1·6	0·2	0·15	0·35	0·95	0·85	0·5	0·75	0·4
	*	1·5	2·05	0·25	0·2	0·4	1·25	1·05	0·75	1·05	0·55
	*	1·5	2·2	0·2	0·25	0·5	1·4?	1·15?	0·7	1·1?	0·65
	*	1·8	2·6	0·35	0·35	0·5	1·4	1·25?	0·6?	1·2?	0·5
	*	1·85	2·6	0·25	0·3	0·5	1·75	1·45	0·85	1·5	0·6
megalops		**2·9**	**3·85**?	**0·55**	—	**0·75**?	**2·8**	—	**1·55**?	**2·1**	**1·1**
topotypes		3·1	—	0·55	—	—	2·85	2·4	1·5	2·25	1·3
		3·35	4·6	0·6	0·5	0·95	3·0	—	1·55	2·25	1·3

Pygidium

1 to 8 as for Proetidae (p. 219)

Variates		1	2	3	4	5	6	7	8
Individual	*	0·95	0·55	(*2·15*)	0·55	0·35	4·2	0·07	0·07
specimens		1·35	0·75	(*3·05*)	0·75	0·45	4·4	0·12	0·10
		1·35	0·8	3·0	0·9	0·4	4·6	0·12	0·12

REMARKS. Two cranidia (It 5049 illustrated on Pl. 5, fig. 22; the other fragmentary) differ from other Keisley specimens in having a less inflated glabella with short (exsag.) basal lobes and tapering forwards to a sub-triangular preglabellar furrow, features which suggest comparison with *O. trigoda* Warburg sp. (1925 : 190, pl. 5, figs. 38–39).

Comparison of the Keisley cranidia with the original topotype material of M'Coy's species (redescribed by Whittington & Campbell 1967 : 461, pl. 19, figs. 1–11) is made difficult by the larger size of the Irish specimens. The effect of the size difference may in principle be overcome, on the assumption that the size eigenvector of the Keisley specimens would not change significantly at sizes larger than the largest cranidium in the sample, by comparisons of the scores of the Keisley and Irish specimens on the shape eigenvectors of the Keisley sample. However, the small size of the latter sample (7 complete specimens if variate 7 is excluded) and the fact that several of the specimens are distorted (albeit slightly) both affect adversely the accuracy of the sample estimates of the eigenvectors, and, when considerable size extrapolation is involved (from Keisley to Irish specimens), inaccuracy in the estimated size eigenvector will introduce a size element into intended shape comparisons along sample shape eigenvectors. Nevertheless, with all its limitations and inaccuracies, plotting of the specimens along the Keisley shape eigenvectors is a considerably better method of bridging the size gap between the two samples than either an intuitive assessment of changing cranidial proportions or the comparison of photographs enlarged to the same size, for the first of these alternatives is subjective as well as being excessively difficult while the second is illegitimate in that it takes no account of changing proportions. The scores of the two most complete Irish specimens (variate 4 being estimated on the holotype) on the second eigenvector of the Keisley 9-variate variance-co-

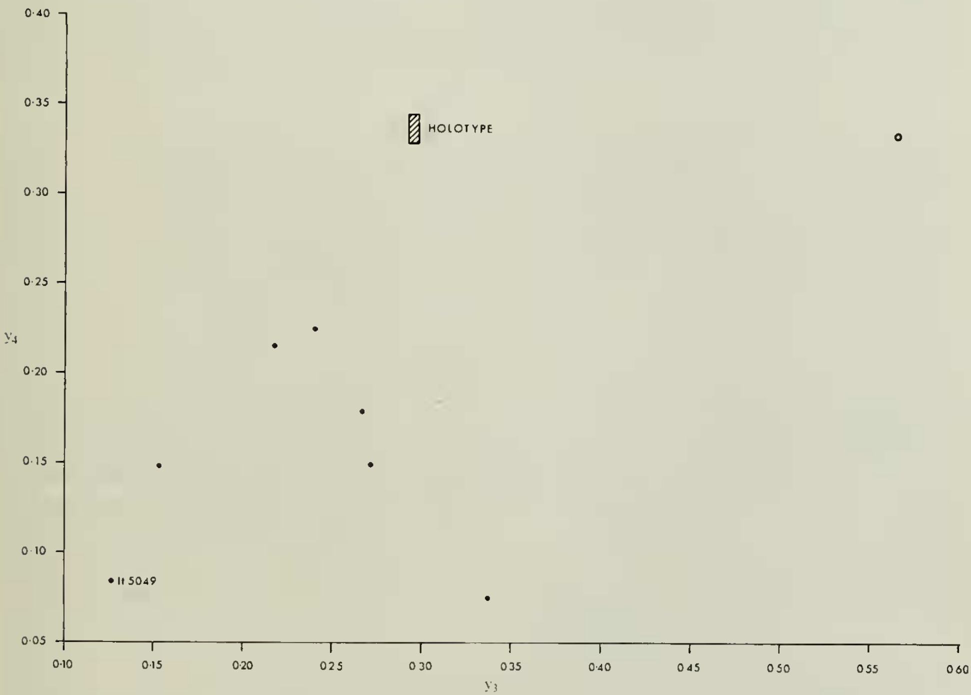

FIG. 4. Cranidia of *Otarion megalops* from Keisley (closed circles) and Ireland (holotype indicated; open circle is another topotype) plotted on the third (y_3) and fourth (y_4) eigenvectors of the variance-covariance matrix of the Keisley specimens. Transformed scale units correspond to original measurements in mm. See text for further explanation.

variance matrix almost straddle the spread of Keisley values, but for both the third and fourth eigenvectors the Irish specimens lie beyond the Keisley range (Text-fig. 4). The direction cosines of the maximum shape difference between the two samples relative to the Keisley size eigenvector for variates 1, 2, 3, 4, 5, 6, 8, 9 and 10 are (0·39, −0·01, 0·27, −0·17, −0·02, −0·01, 0·35, −0·66, 0·43). The Irish specimens may therefore, when allowance is made for the size difference, have glabellas which are narrower at the distal ends of S_1 and somewhat longer, with somewhat longer and narrower (tr.) basal lobes. It is interesting that, relative to y_3 and y_4, specimen It 5049 differs from other Keisley specimens in a direction opposite to that in which the Irish specimens differ; there appears, though, to be no reason for separating it from the rest of the sample.

An external mould of a cranidium on the same block as the holotype of *O. megalops* shows that the outer surface of the glabella, and possibly also of the pre-glabellar field, of the Irish species is finely tuberculate, in contrast to the smooth outer surface of the Keisley specimens.

In summary, accurate comparison of the Keisley specimens with *O. megalops* is not possible because of the size discrepancy, but such limited analysis as is possible indicates relatively slight differences and the Keisley material is referred to M'Coy's species. Attribution of the Keisley pygidia to *O. megalops* is provisional.

Family **AULACOPLEURIDAE** Angelin 1854

Genus ***AULACOPLEURA*** Hawle & Corda 1847

Type species. *Arethusa Koninckii* Barrande 1846 by monotypy.

Aulacopleura sp.

(Pl. 5, fig. 23)

A single fragmentary cranidium shows a short tapering glabella reaching a little over half the length of the cephalon and with strongly cut-off basal lobes, a thin eye-ridge, long horizontally disposed pre-glabellar field, broad anterior border furrow, and narrow upturned anterior border. The entire surface except for the furrows and the crest of the anterior border is covered with rounded tubercles about 0·125 mm. across at their bases.

The specimen is too poor for useful comparisons to be made. The strongly tuberculate surface is unusual in *Aulacopleura*.

Measurements.

sagittal length of pre-occipital glabella (normal projection), 2·6

mid-point of occipital furrow to anterior margin of cranidium (sag.) (projected as above), 5·0

mid-point of occipital furrow to distal end of S_1 (exsag.) (projected as above), 1·15

Family **CALYMENIDAE** Burmeister 1843

Genus ***FLEXICALYMENE*** Shirley 1936

Type species. *Calymene Blumenbachii* var. *Caractaci* Salter 1865 by original designation of Shirley (1936 : 395).

Flexicalymene sp.

(Pl. 6, figs. 1–17)

DESCRIPTION. *Cranidium* : Glabella reaches further forward than cheeks. No pre-glabellar field. Anterior border slopes slightly up forwards relative to tangent plane to posterior part (i.e. that opposite L_1 and L_2) of pre-occipital glabella ; anterior border slightly concave in section near border furrow, becoming convex towards margin. Well-developed anterior pit opposite frontal lobe of glabella ; faint transverse ridge sometimes observable across axial furrow behind anterior pit. Palpebral lobe opposite S_2 and L_2 in largest forms, relatively further forward in smaller forms. Relative dimensions of glabella and disposition of glabellar furrows are summarized in quoted measurements. S_3 faint.

Free cheek : Apparently almost vertically disposed. Visual surface not known ; base of eye passing gradually into cheek which has slight independent convexity. Border furrow broad. Border slopes outwards from steep inward (horizontal in life) slope adjoining border furrow ; border slightly convex in section, widening forwards along cheek margin. Doublure slightly narrower than border (and also widening forwards along cheek margin), disposed almost parallel to overall surface of cheek, slightly concave dorsally ; outer surface of doublure apparently smooth.

Hypostome : Anterior margin convex, posterior margin embayed. Minimum width at about mid-length. Middle body strongly convex, highest at about mid-length of anterior lobe ; middle body vaguely delimited anterolaterally, separated from anterior border axially by short (tr.) depression, more sharply defined posteriorly where posterior furrow reaches nearly to posterior margin axially ; middle body narrowest at about mid-length. Middle furrow continuous across axial line, running close and almost parallel to lateral-posterior furrow, cutting off narrow sub-crescentic posterior lobe with slight independent convexity. Anterior furrow vague ; anterior border turned almost vertically up (ventrally) and continued dorsolaterally into anterior wing which bears dorsolaterally directed sub-circular process. Lateral border narrow and high opposite mid-length of middle body, widening and flattening behind posterior wing towards pointed posterior prolongation. Doublure vertical opposite midlength of middle body, becoming overturned near posterior wing which is developed as a transverse ridge on dorsal surface of doublure. Outer surface of hypostome (except apparently anterior part of middle body) faintly granular.

Thoracic segment: Pleura with sharp transversely directed pleural furrow turning slightly back just before dying out near spatulate pleural tip. Posterior band considerably wider than anterior band; anterior band widening rapidly at its distal end towards pleural tip. Doublure of posterior pleural margin long, its inner margin sub-parallel to pleural furrow and then curving round parallel to tip of pleura; doublure of anterior pleural margin short, terminating abruptly and shortly inwards; doublure flat posteriorly and laterally, raised (ventrally) to form vincular notch outside anterior termination.

Pygidium: Width of axis at anterior margin forming 34·6, 39·1, 41·5 per cent of maximum pygidial width in three specimens. Axis with 5 or 6 rings defined by ring furrows and traces of at least one further ring indicated by row of tubercles. Pleural lobes with 5 distinguishable segments. Pleural furrows deeper and more curved than interpleural furrows (on internal moulds pleural furrows deep and conspicuous, interpleural furrows very faint, particularly proximally). Anterior pleural bands nearly parallel-sided, widening towards distal ends; posterior bands wider than anterior bands except at distal ends where widths of bands become sub-equal; both bands equally but not greatly convex. Doublure narrow, inclined upwards inwardly; outer surface of doublure apparently smooth.

Dorsal surface: Entire dorsal surface (except furrows) bears tubercles, closest and strongest around the periphery of the complete integument, i.e. at margins of anterior border and free cheeks, at tips of pleurae, and around lateral and posterior margins of pygidium. The tubercles are associated with approximately parallel-sided pores which also are strongest peripherally where they can be seen to pierce the integument. In pygidia about 1·5 mm. long the pleural tubercles form a single row on each of the anterior and posterior pleural bands; in slightly larger pygidia there is a single row on the anterior band and two rows roughly alternating in position on the posterior band; in the largest pygidia additional tubercles mask this arrangement.

MEASUREMENTS.

Cranidium (all lengths projected as 1)

1 = sagittal length of cranidium (normal projection)
2 = sagittal length of anterior border (measured on internal mould to vertical anterior margin of glabella)
3 = sagittal length of pre-occipital glabella (see 2)
4 = sagittal length of occipital ring
5 = mid-point of occipital furrow to posterior margin of eye (exsag.)
6 = mid-point of occipital furrow to anterior pit (exsag.)
7 = mid-point of occipital furrow to distal end of S_3 (exsag.)
8 = mid-point of occipital furrow to distal end of S_2 (exsag.)
9 = mid-point of occipital furrow to distal end of S_1 (exsag.)
10 = transverse separation of anterior pits
11 = transverse separation of distal ends of S_3
12 = transverse separation of distal ends of S_2
13 = transverse separation of distal ends of S_1
14 = width of glabella (maximum) across L_1

N.B. When the glabellar furrow does not reach the axial furrow the ' distal end ' in 7–9 and 11–13 is the point where the projection of the glabellar furrow along its length meets the axial furrow.

Variates		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Individual	*	1·55	0·2	1·1	0·2	0·55	0·85	0·7	0·55	0·4	0·65	—	0·65	0·65	0·7
specimens		1·6	0·2	1·2	0·25	0·5	0·85	0·75	0·55	0·35	0·85	0·85	0·9	0·9	0·95
	*	2·95	0·5	1·95	0·5	0·95	1·5	1·3	1·15	0·75	1·5	1·55	1·65	1·75	1·85
	*	4·25	0·75	2·85	0·65	1·2	2·25	2·0	1·65	1·05	1·75	—	2·0	2·25	2·4

Hypostome (all lengths projected as 15)

15 = sagittal length (normal projection)
16 = overall length (exsag.)
17 = anterior margin to middle furrow (sag.)
18 = sagittal length of posterior lobe of middle body
19 = width of hypostome at posterior wings
20 = width of hypostome at anterior wings (excluding processes)
21 = minimum width of hypostome

Variates		15	16	17	18	19	20	21
Individual		—	—	—	0·3	0·85	—	0·75
specimens	*	1·3	—	1·0	0·25	0·95	1·2	0·85
	*	1·35	1·45	1·0	0·25	—	—	0·95
	*	2·35	—	1·85	0·4	—	2·25	—
		—	—	—	0·5	(*2·1*)	—	1·75
		2·9	3·15	2·35	0·45	—	2·65	1·8

Pygidium (all lengths projected as 22)

22 = sagittal length excluding half-ring (normal projection)
23 = 22 minus thickness of integument
24 = sagittal length of axis excluding half-ring
25 = articulating furrow to ring furrow behind 5th axial ring (sag.)
26 = maximum width minus thickness of integument
27 = width of axis at anterior margin
28 = width of axis at ring furrow behind 5th axial ring
29 = width (perpendicular to length of pleura) of anterior band of 2nd pleura at mid-length of pleura (projected normal to pleura)
30 = width (perpendicular to length of pleura) of posterior band of 2nd pleura at mid-length of pleura (projected as 29)
31 = score of sutural furrow behind 3rd pleura on scale of distal ends of ring furrows (articulating furrow counted as 1)

Variates		22	23	24	25	26	27	28	29	30	31
Individual	*	—	1·35	—	0·95	2·55	1·0	0·5	0·12	0·12	—
specimens	*	—	1·5	1·3	—	3·2	1·1	—	—	—	—
		2·65	2·55	2·3	1·55	—	1·55	1·25	0·18	0·19	4·2
	*	3·6	3·4	3·1	—	(*5·8*)	2·4	—	—	—	—
		—	4·35	3·7	—	—	3·2	2·1	—	—	4·0
	*	—	4·65?	4·0	—	—	2·8	—	—	—	—
	*	—	—	—	—	—	—	—	0·27	0·39	—

ONTOGENY. Two small cranidia are known, 1·55 mm. and 1·6 mm. long respectively (Pl. 6, figs. 10, 11, 14). In these specimens the glabella is parallel-sided, the frontal lobe is proportionately long, there is a strong axial occipital tubercle, and the anterior border bears many small tubercles (of which in the smaller specimen two situated shortly within the prolongations of the axial furrows are prominent); the larger specimen appears to have a fixigenal spine. The strong occipital tubercle is not distinguishable in a cranidium 2·95 mm. long.

REMARKS. Accurate comparison of the Keisley species must await quantitative description of topotype material of such species as *F. caractaci* (Salter) and *F. cobboldi* Dean (see Dean 1963 : 217, 218). The Keisley material, although well preserved and allowing detailed qualitative description of much of the exoskeleton, is not considered abundant enough to form the basis for the erection of a new species.

There are too few cranidia to show whether the variation in glabellar width is discontinuous, but in any case some of the narrower specimens appear to have suffered lateral compression.

Family **DALMANITIDAE** Vogdes 1890

Genus ***DALMANITINA*** Reed 1905

TYPE SPECIES. *Phacops socialis* Barrande, 1846 by original designation of Reed (1905b : 224).

Dalmanitina mucronata brevispina Temple, 1952

(Pl. 5, figs. 6, 14, 24–26)

1952 *Dalmanitina mucronata* (Brongniart) var. *brevispina* Temple : 14, pl. 2, fig. 2.
1952 *Dalmanitina mucronata* var. *brevispina* Temple ; Temple : 16.

HOLOTYPE. Internal and external moulds of pygidium, A 36372a,b figured by Temple 1952 : pl. 2, fig. 2, from basal Silurian, Watley Gill, Cautley, Yorkshire.

REMARKS. This subspecies was described qualitatively in 1952 on the basis of material from Yorkshire. Measurements of topotype material are given here together with measurements of specimens from Keisley. The two collections, however, are small, and both the quantitative distinction of the subspecies from *D. mucronata mucronata* and the identity of the Yorkshire and Keisley forms should be considered only provisional.

In Keisley specimens the surface is seen to bear small tubercles. The terminal pygidial spine is variable in length and not always thorn-like. Two protaspides are known.

MEASUREMENTS.

Cranidium (all lengths projected as 1)

1 = sagittal length of glabella (normal projection)
2 = sagittal length of occipital ring
3 = mid-point of occipital furrow to inner end of S_3 (exsag.)
4 = inner end of S_3 to mid-point of pre-glabellar furrow (exsag.)
5 = maximum length (exsag.) of palpebral lobe
6 = maximum width of glabella
7 = maximum width (tr.) of occipital ring

8 = maximum transverse separation of outer margins of palpebral lobes
9 = posteriormost point of outer margin of palpebral lobe to posterior margin of cheek in exsagittal line
10 = score of transverse projection of posteriormost point of outer margin of palpebral lobe on scale of distal ends of glabellar furrows (occipital furrow counted as 0)

Variates		1	2	3	4	5	6	7	8	9	10
Individual		1·9	0·35	0·7	0·85	0·95	1·6	—	—	—	—
specimens		2·8	0·45	1·0	1·35	1·1	2·15	(*1·25*)	—	0·55	—
	*	4·25	0·55	1·25	2·5	1·3	—	1·65	4·25	0·45	0·25
brevispina paratype		5·6	0·8	1·75	3·05	—	4·6	2·6	(*6·9*)	—	—

Pygidium

11 = sagittal length excluding half-ring but including terminal spine (normal projection)
12 = articulating furrow to ring furrow behind 6th axial ring (sag.) (projected as 11)
13 = maximum width
14 = width of axis at anterior margin
15 = width of axis at ring furrow behind 6th axial ring
16 = width (perpendicular to length of pleura) of anterior band of 4th pleura at mid-length of pleura (projected normal to pleura)
17 = width (perpendicular to length of pleura) of posterior band of 4th pleura at mid-length of pleura (projected as 16)
18 = score of sutural furrow behind 5th pleura on scale of distal ends of ring furrows (articulating furrow counted as 1)

Variates		11	12	13	14	15	16	17	18
Individual		—	0·8	—	—	0·35	0·07	0·05	6·3
specimens	*	3·15	1·55	3·2	1·05	0·65	0·15	0·13	6·2
	*	—	1·95	5·0	1·4	0·75?	0·21	0·19	6·1
		—	2·15	—	—	1·0	—	—	6·2
brevispina		**4·35+**	**2·4**	(**6·1?**)	**2·0**	**1·25**	**0·21**	**0·26**	**6·2**
topotypes		—	2·4	(6·7?)	2·0	1·2	0·24	0·27	6·1

VIII. REFERENCES

Bruton, D. L. 1967. Silurian odontopleurid trilobites from Sweden, Estonia, and Latvia. *Palaeontology*, London **10** : 214–244, pls. 30–36.

Burnaby, T. P. 1966. Growth-invariant discriminant functions and generalized distances. *Biometrics*, **22** : 96–110.

Dalman, J. W. 1827. Om Palaeaderna, eller de så kallade Trilobiterna. *K. svenska Vetensk-Akad. Handl.* Upsala & Stockholm, **1** : 226–294, pls. 1–6.

Dean, W. T. 1963. The Ordovician trilobite faunas of South Shropshire, III. *Bull. Brit. Mus. (Nat. Hist.) Geol.* London **7** : 213–254, pls. 37–46.

HAVLÍČEK, V. & VANEK, J. 1966. The Biostratigraphy of the Ordovician of Bohemia. *Sborn. geol. věd. Praha*, Praha, [P], **8** : 7–68, pls. 1–16.
JAANUSSON, V. 1956. On the Trilobite Genus *Celmus* Angelin, 1854. *Bull. geol. Instn Univ. Upsala*, Upsala **36** : 35–49, pl. 1.
KIELAN, Z. 1960. Upper Ordovician trilobites from Poland and some related forms from Bohemia and Scandinavia. *Palaeont. pol.*, Warsawa **11** : i–vi, 1–198, pls. 1–36.
M'COY, F. 1846. *A Synopsis of the Silurian Fossils of Ireland collected from the several districts by Richard Griffith, F.G.S.* 72 pp., 5 pls. Dublin.
REED, F. R. C. 1896. The Fauna of the Keisley Limestone.—Part I. *Q. Jl geol. Soc. Lond.*, London **52** : 407–437, pls. 20–21.
—— 1902. Notes on the genus *Lichas*. *Ibid.*, **58** : 59–82.
—— 1905a. New fossils from the Haverfordwest district. III. *Geol. Mag.*, London & Hertford, dec. 5, **2** : 97–104, pl. 4.
—— 1905b. The classification of the Phacopidae. *Ibid.* dec. 5, **2** : 224–228.
—— 1907. The base of the Silurian near Haverfordwest. *Ibid.* dec. 5, **4** : 535–537.
RICHTER, R. & E. 1917. Über die Einteilung der Familie Acidaspidae und über einige ihrer devonischer Vertreter. *Zentbl. Miner. Geol. Paläont.*, Stuttgart Jahrg. 1917 : 462–472.
—— 1926 Beiträge zur Kenntnis devonischer Trilobiten IV. Die Trilobiten des Oberdevons. *Abh. preuss. geol. Landesanst.*, Berlin [NF], **99** : 1–314, pls. 1–12.
SHAW, A. B. 1957. Quantitative trilobite studies II. Measurement of the dorsal shell of non-agnostidean trilobites. *J. Paleont.*, Tulsa **31** : 193–207.
SHAW, F. C. & ORMISTON, A. R. 1964. The eye socle of trilobites. *J. Paleont.*, Tulsa **34** : 1001–2.
SHIRLEY, J. 1936. Some British Trilobites of the Family Calymenidae. *Q. Jl geol. Soc. Lond.*, London **92** : 384–421, pls. 29–31.
TEMPLE, J. T. 1952. A revision of the trilobite *Dalmanitina mucronata* (Brongniart) and related species. *Acta Univ. Lund.*, Lund, [NF], (2), **48** : 1–33, pls. 1–4.
—— 1968. The Lower Llandovery (Silurian) brachiopods from Keisley, Westmorland. *Palaeontogr. Soc.* [*Monogr.*], London No. 521 : 1–58, pls. 1–10.
WAHLENBERG, G. 1818. Petrifacta Telluris Svecanae. *Nova Acta R. Soc. Sci. upsal.*, Upsala **8** : 1–116, pls. 1–4.
WARBURG, E. 1925. The Trilobites of the Leptaena Limestone in Dalarne. *Bull. geol. Instn Univ. Upsala*, Upsala **17** : i–viii, 1–446, pls. 1–11.
—— 1939. The Swedish Ordovician and Lower Silurian Lichidae. *K. svenska VetenskAkad. Handl.*, Upsala & Stockholm **17** : 1–162, pls. 1–14.
WHITTINGTON, H. B. 1941. Silicified Trenton Trilobites. *J. Paleont.*, Tulsa **15** : 492–522, pls. 72–75.
—— 1956. Silicified Middle Ordovician trilobites : The Odontopleuridae. *Bull. Mus. comp. zool. Harv.*, Cambridge, Mass. **114** : 155–288, pls. 1–24.
—— 1957. The ontogeny of trilobites. *Biol. Rev.*, Cambridge **32** : 421–469.
—— 1966. A Monograph of the Ordovician trilobites of the Bala area, Merioneth. Part III. *Palaeontogr. Soc.* [*Monogr.*], London No. 512 : 63–92, pls. 19–28.
—— & CAMPBELL, K. S. W. 1967. Silicified Silurian Trilobites from Maine. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass. **135** : 447–482, pls. 1–19.
—— & EVITT, W. R. 1954. Silicified Middle Ordovician Trilobites. *Mem. geol. Soc. Amer.*, Washington, **59** : 1–137, pls. 1–33.

J. T. TEMPLE M.A., Ph.D.
Department of Geology
BIRKBECK COLLEGE
MALET STREET
LONDON, W.C.1